Z. Säugetierkunde 58 (1993) 48–53

ISSN 0044-3468

Size variation in *Rhabdomys pumilio:* A case of character release?

By Y. Yom-Tov

J. R. Ellerman Museum, Department of Zoology, University of Stellenbosch, Stellenbosch, South Africa and Department of Zoology, Tel Aviv University, Tel Aviv, Israel

Receipt of Ms. 4. 2. 1992
Acceptance of Ms. 24. 2. 1992

Abstract

Studied size variation in the striped mouse *Rhabdomys pumilio,* a diurnal herbivorous murid, across southern Africa using the greatest length of the skull (GTL) as a measure of body size. There was a positive correlation between GTL and the mean minimum temperature of the coldest month (July), contrary to Bergmann's rule, but there was no significant correlation between GTL and either mean maximal annual temperature, mean maximal temperature of the hottest month (January), altitude or annual rainfall. There were differences in size between samples of different biotic regions: Animals from the south west Cape were largest, followed by those from the Namib desert, forest, south west arid zone, and the savanna, respectively.

Animals from the zone of sympatry with *Lemniscomys griselda,* a larger herbivorous diurnal murid, were significantly smaller than those from allopatric zones. It is suggested that character release is a primary factor in determining body size of *R. pumilio* in southern Africa.

Introduction

The striped mouse *Rhabdomys pumilio* is a small (30–35 g), diurnal murid which is widely distributed in eastern and southern Africa. It occupies a wide range of habitats, all of which have some cover of grass, at latitudes of up to 1800 m above sea level in Zimbabwe (Smithers 1983), but avoids tropical woodland savannas and parts of the central Karoo where there is no grass (De Graaf 1981). Throughout its large distribution area it varies greatly in colour and size. This situation led to conflicting conclusions regarding its taxonomic state: Roberts (1951) recognized 20 subspecies for the southern Africa subregion alone while others stated that their status is doubtful (Meester et al. 1986). Coetzee (1970) came to the conclusion that it is impossible to recognize subspecies and that at the most there is a pale coloured western and a dark coloured eastern form. Some morphological trends were determined: Specimens from the Cape Province are larger than those from Zimbabwe (Roberts 1951) and specimens from high altitudes in the Drakensberg Mountains have shorter tails than those from lower altitudes (Rowe-Rowe and Meester 1985). The genus is monospecific.

Size variation in mammals and other animals has been correlated with several abiotic and biotic factors. Among the abiotic factors, probably the most commonly mentioned in the literature are those which relate body size or the relative size of body extremities (legs, tails and ears) to ambient temperature. According to the rule of Bergmann (1847), races of warm blooded animals which live in warm climates have smaller body size than their relatives which live in cold climates (Mayr 1970). Body size might be correlated with food availability, as have been shown by Yom-Tov and Nix (1986). It might also be influenced by interspecific competition, either through character displacement or character release (Brown and Wilson 1956; Lincoln et al. 1982).

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5801-0048 $ 02.50/0

The aim of this paper is to discern which factor or factors are likely to determine the variation which exists in body size between the southern African populations of *R. pumilio*.

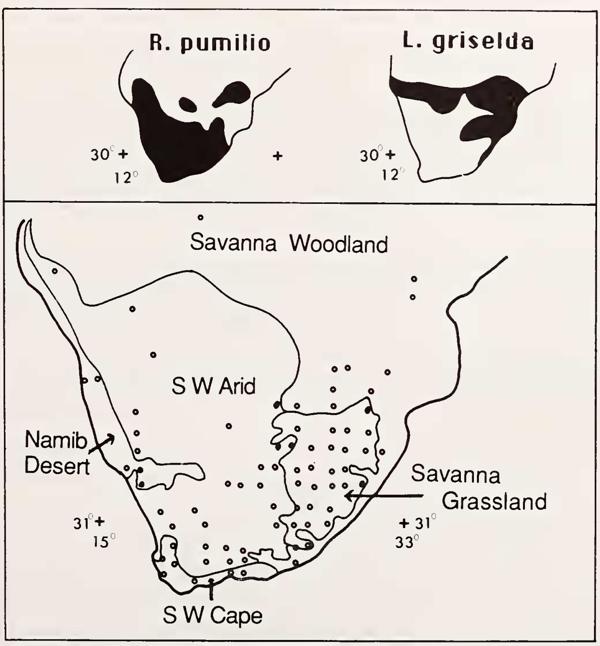
Material and methods

Skulls of adults which have been collected in South Africa, Namibia, Botswana, Zimbabwe and Lesotho, were measured in the following museums in South Africa: The John Ellerman Museum, University of Stellenbosch; South African Museum, Capetown; The Kaffarian Museum, King William's Town; The National Museum, Bloemfontein; and the Transvaal Museum, Pretoria. The geographical range of the specimens in this study ranged from 18° S in Namibia and Zimbabwe to 34° 29′ S in the Cape Province of South Africa and from 13° E in Namibia to 32° 40′ E in Zimbabwe.

In this study the skull length was used as a comparative measure of body size. The greatest length of the skull (GTL) in its midline from the front of the upper incisors to the posterior margins of the skull was measured with digital calipers to accuracy of 0.01 mm. Only skulls with complete fusion of the bones and fully grown teeth were measured. Since no sexual dimorphism in size was detected in this species (Smithers 1983), the data for males and females were pooled.

The desired sample size for this study was to obtain 20 specimens from each degree square of southern Africa, south of 18° S. There are about 280 such squares, but specimens were available for only 77 (Figure). The best represented areas were those south and east of the line stretching from the south west Cape province (30° S 17° E) to north east Natal (20° S 30° E) which contains about 120 squares of which 63 contained samples. However, there were very large areas, especially in the Kalahari Desert, from which no specimens were available. For some squares which vary greatly in latitude more than one sample was measured, so that altogether there are 92 samples from 85 degree squares in this study, totaling 1260 specimens.

Climatological data were taken from the nearest weather station to the locality of each sample, using long term data published by the South African Weather Bureau (Climate of South Africa 1986). Some of the specimens, mainly from areas which are densely populated by humans, came from localities which were within a range of a few kms from a weather station, but many others,



Biotic zones of southern Africa (after Davis 1962) and locations of the samples measured in this study. The upper maps are the distribution areas of *Rhabdomys pumilio* and *Lemniscomys griselda* (after Smithers 1983). Forest areas are not marked on the map, as they are too small. Circles indicate locations of the 77 samples examined in this study particularly from remote localities in Namibia and Botswana, were collected many kms from the nearest weather station. However, since these areas generally consist of wide plains, it is likely that the data from the nearest weather station does not differ much from the actual local weather.

The means of GTL of each sample were regressed against the following climatological data: mean annual rainfall, mean maximal annual temperature, mean maximal temperature of the warmest month (January) and mean minimal temperature of the coldest month (July).

In order to examine the possibility that altitude affects skull size, one degree square (31° S 27° E) which varies greatly in altitude (1000–2100 m above sea level), was sub-divided into 16 quarter degrees squares. For 10 of these squares there were samples of skulls (4–20 in each, mean = 12.7), for each of which the mean of their GTL was calculated and regressed against the altitude from which the skulls were collected.

Southern Africa can be geographically subdivided into different biotic zones, differing from each other climatologically and vegetationally. The classification used in this study is that used by Meester (1965, after Keay 1959 and Davis 1962).

In order to test the possibility that body size of *Rhabdomys* is different in zones of sympatry and allopatry with *Lemniscomys*, mean GTL was calculated for these zones using the distribution maps for these species in Smithers (1983).

Results

There was no significant correlation between GTL and either annual rainfall, altitude, mean maximal temperature in January or mean maximal annual temperature, but contrary to Bergmann's rule, there was a positive significant correlation between GTL and mean minimal temperature of the coldest month (July, $r = 0.6679$; $p = 0.009$). Mean GTL is 29.88 and 28.42 mm in areas where mean minimal July temperatures are −3 °C and 10 °C, respectively.

There were differences in skull size between samples of different biotic regions. The largest skulls belonged to animals from the south west Cape, followed by those from the Namib desert, forest, south west arid zone and the savanna (grassland and woodland), in this order (Tab. 1). There was little variation in size within each zone, the coefficient of variation ranged between 1.4–4.1 %. Animals from the south west Cape were significantly larger than those from all other zones except the forest, and those of the savanna were significantly smaller than animals from all other zones. There were also some significant differences between the other groups (Tab. 2).

Mean GTL (and standard deviation) of *Rhabdomys* in the zones of sympatry and allopatry with *Lemniscomys* are 26.0 (SD = 0.7; range 24.4–27.4; n = 26) and 27.3 mm (SD = 1.0; range 25.5–29.6; n = 58), respectively.

The correlation between GTL and mean minimal July temperature became higher ($r = 0.9267$; $p = 0.0001$) when run without the samples from locations where *Rhabdomys* is sympatric with *Lemniscomys* (i.e. only on allopatric samples). This was due to the fact that GTL of samples from areas of sympatry was smaller and came from relatively warmer (northern) areas in southern Africa. However, there was no significant correlation between any of the examined temperature parameters and GTL of the samples taken from areas of sympatry only.

Discussion

Bergmann's rule predicts that warm blooded animals which live in cold regions are larger than those of the same species which live in warm areas, i.e. a negative correlation is predicted between body size and ambient temperature. GTL of the striped mouse is not correlated with mean annual maximal temperature or mean maximal temperature of the warmest month, and, contrary to the predication of Bergmann's rule, it is positively correlated with mean minimal temperature in July.

Yom-Tov and Nix (1986) have shown that biomass productivity is correlated with body size in three species of Australian mammals. Different biotic zones often have

Table 1. **Mean and standard deviation (SD) and the coefficient of variation (CV, %) of GTL of *Rhabdomys pumilio* in various biotic zones of southern Africa**

Zone	n, groups	n, specimens	Mean	SD	CV
Namib	5	76	28.0	0.4	1.4
South West Cape	7	108	28.7	0.6	2.1
Forest	4	52	27.9	1.1	4.1
South West Arid	27	380	27.2	0.7	2.5
Southern Savanna	30	472	26.2	0.7	2.8
Southern Savanna Woodland	12	172	26.1	0.6	2.4
Total	85	1260			

Table 2. **Results of T-test comparing mean GTL of the various biotic zones of southern Africa**
In each comparison the upper figure is the t value, the lower its probability. NS – Not significant

Zone	SW Cape	Forest	SW Arid	Southern Savanna Grassland	Southern Savanna Woodland
Namib	2.4 0.05	1.8 NS	3.6 0.001	8.57 0.001	7.6 0.001
SW Cape		1.36 NS	5.76 0.001	9.61 0.001	9.29 0.001
Forest			1.25 NS	3.04 0.01	3.16 0.01
NW Arid				5.56 0.001	4.45 0.001
S Savanna Grassland					0.48 NS

different productivity, to which body size might be correlated. There have been various attempts to subdivide Southern Africa into biotic zones, but Davis's (1962) classification is the most accepted today (Meester 1965; Rautenbach 1978). According to this classification there are four biotic zones in this region, two of which are subdivided into two distinct subregions (totalling six zones):

Southern savanna which encompasses the wetter eastern part of southern Africa, with more than 500 mm annual rainfall. This zone has two distinct subregions – grassland in its south and woodland in the north and the eastern coast.

South West Arid which consists of the arid western part of southern Africa, with a mean annual rainfall less than 500 mm. The Namib desert of the western coastal strip is recognized as a distinct subregion.

Forest, which consists of isolated patches of montane and subtropical evergreen forest in the savanna and west Cape regions.

South West Cape, a climatically and biotically distinct zone which corresponds to the Cape macchia.

In southern Africa, as in other dry environments, precipitation is associated with primary production. Since GTL is not correlated with rainfall, it does not appear that primary production affects size in the striped mouse.

By way of elimination, the above findings indicate that the factor which determines the significant differences in GTL is biotic rather than abiotic. Among the biotic factors, interspecific competition, particularly over food, was shown to affect size in various animals. Character displacement is a situation in which, where two species of animals overlap geographically, the differences in size between them are accentuated in the zone of sympatry and weakened or lost in the parts of their ranges outside this zone (Brown and Wilson 1956). This phenomenon arises from competition between the two, and the removal of the larger of the two species may be followed by an increase in the variation in some phenotypic character, a situation termed character release (Lincoln et al. 1982). Recently, Alcantara (1991) has shown that there is an increase from north to south in body size of the wood mouse *Apodemus sylvaticus,* contrary to Bergmann's rule, and he raised the possibility that body size of the wood mouse is determined by competition with the yellow-necked mouse *Apodemus flavicollis.* If *R. pumilio* has a competitor, it is likely to be another diurnal rodent, similar in size, habitat and habits. There are two other genera of diurnal rodents in southern Africa, *Otomys* (seven species) and *Lemniscomys* (one species: *L. griselda*). All species of *Otomys* present in southern Africa are considerably larger than the other two diurnal genera, with body weight averaging above 100 g, while *Lemniscomys* weighs on average 58 g and *Rhabdomys* between 37–54 g (Smithers 1983). Moreover, the preferred habitats of *Otomys* are fringes of swamps, wet vleis and other wet grassy habitats while the other two diurnal rodents prefer dense grass. Both factors make *Otomys* species unlikely competitors with the other two diurnal species. However, the other two genera are very similar: both belong to the Murinae, prefer the same habitat (dense grass) and are largely granivorous (*Otomys* is largely herbivorous). The only consistent anatomical difference between *Lemniscomys* and *Rhabdomys* would seem to be that *Lemniscomys* has a much reduced fifth digit in the forefoot while *Rhabdomys* has five normal digits (Roberts 1951). *Lemniscomys* is slightly larger than *Rhabdomys* (GTL ranges between 30.5–35.5 and 26.0–30.8 mm, respectively; Roberts 1951), and it is reasonable to assume that it will be more successful when competing with the smaller *Rhabdomys* where they are sympatric.

I suggest that the relatively large GTL of the striped mouse in the south-west Cape, forest and the Namib desert relative to that in the savanna might be explained as a case of character release. The distribution areas of the two genera in southern Africa overlap to some extent: While *Rhabdomys* occurs in all six biogeographic zones of southern Africa, *Lemniscomys* occupies the southern savanna woodland, the northern part of the grassland and the northern areas of the south west arid zone (Smithers 1983), where the two species are sympatric. It is reasonable to assume that *Rhabdomys* is larger in areas where it is allopatric with *Lemniscomys* due to the absence of its larger competitor, i.e. due to character release. This situation is remarkably similar to that found recently by Alcantara (1991) for wood mice in Europe: In both studies the size of the smaller species of the two possible competitors (*Apodemus sylvaticus* in Europe, *Rhabdomys pumilio* in southern Africa) is positively correlated with ambient temperature, contrary to Bergmann's rule, and in both size increases in the zones of allopatry with the potential competitor (*A. flavicollis* in Europe, *Lemniscomys griselda* in southern Africa).

Acknowledgements

This work would not have been possible without the help given to me by many people in South Africa. I would like to express my gratitude to Prof. Jan Nel, Head of the Zoology Department of Stellenbosch University for his exceptional hospitality in Stellenbosch; Drs. Graham Avery of the National Museum, Capetown; Richard Klein of Chicago University; Lloyd Wingate of the Kaffarian Museum, King William's Town; Johan Watson of the National Museum, Bloemfontein; Naas Rautenbach, Director of the Transvaal Museum, Pretoria; Prof. John Skinner and Prof. Rudi van Aarde of the Mammal Research Institute, University of Pretoria – all provided hospitality and help in many ways. I am grateful to them all for making my stay in South Africa enjoyable and productive. Thanks are also due to Mrs. Kristie Nel, Mr. Piet Beukes, Mr. Kenneth Payne, Mrs. Richter and the late Mrs. Patsy Skinner for their hospitality. Dr. Tamar Dayan, Dr. Avraham Haim, Prof. H. Mendelssohn and Prof. J. A. J. Nel commented on the manuscript.

This study was supported by the John Ellerman Scholarship, through the University of Stellenbosch.

Zusammenfassung

Die Größenvariation der Streifenmaus Rhabdomys pumilio: ein Fall von Merkmalsfreigabe?

Die Größenvariation der Streifenmaus *Rhabdomys pumilio,* einem tagaktiven herbivoren Nager, wurde im südlichen Afrika untersucht, wobei die größte Schädellänge (GTL) als Maß für die Körpergröße verwendet wurde. Entgegen Bergmanns Regel bestand eine positive Korrelation zwischen der GTL und der mittleren Minimaltemperatur des kältesten Monates (Juli), aber es ließ sich keine signifikante Beziehung zwischen der GTL und dem Jahresmittel der Maximaltemperatur, der mittleren Maximaltemperatur des wärmsten Monates (Januar), der Meereshöhe oder dem Jahresniederschlag belegen. Zwischen Stichproben verschiedener Herkunft bestanden deutliche Unterschiede: am größten waren die Mäuse aus der südwestlichen Kap-Provinz, gefolgt von denen aus der Namibwüste, aus Waldregionen, aus der südwestlichen Trockenzone, und aus Savannen. Tiere aus Regionen sympatrischen Vorkommens, mit *Lemniscomys griselda,* einem vergleichbaren, aber etwas größeren Nager, waren signifikant kleiner als Streifenmäuse aus allopatrischen Teilarealen. Daraus wird geschlossen, daß die Körpergröße von *Rhabdomys pumilio* im südlichen Afrika primär durch Merkmalsfreigabe bestimmt wird.

Literature

South African Weather Bureau (1986): Climate of South Africa. Pretoria: Dep. Environm. Affairs.

Alcantara, M. (1991): Geographical size variation in body size of the Wood mouse *Apodemus sylvaticus* L. Mammal Rev. **21**, 143–150.

Bergmann, C. (1847): Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien **1**, 595–708.

Brown, W. L.; Wilson, E. O. (1956): Character displacement. Syst. Zool. **5**, 49–64.

Coetzee, C. G. (1970): The relative tail length of Striped mouse *Rhabdomys pumilio* Sparrman, 1784 in relation to climate. Zool. Afric. **5**, 1–6.

Davis, D. H. S. (1962): Distribution patterns of Southern African Muridae, with notes on some of their fossil antecedents. Ann. Cape Prov. Mus. **2**, 56–76.

De Graaf, G. (1981): The rodents of Southern Africa. Durban: Butterworths.

Keay, R. W. J. (1959): Vegetation map of Africa south of the Tropic of Cancer. Oxford: Oxford Univ. Press.

Lincoln, R. J.; Boxshall, G. A.; Clark, P. F. (1982): A dictionary of ecology, behaviour and systematics. Cambridge: Cambridge Univ. Press.

Mayr, E. (1970): Population, species and evolution. Cambridge, Mass.: Harvard Univ. Press.

Meester, J. (1965): The origins of the southern African mammal fauna. Zool. Afric. **1**, 87–93.

Meester, J. A. J.; Rautenbach, I. L.; Dippenaar, N. J. D.; Baker, C. M. (1986): Classification of Southern African mammals. Transvaal Mus. Monogr. **5**, 1–359.

Rautenbach, I. L. (1978): A numerical re-appraisal of the southern African biotic zones. Bull. Carnegie Mus. Nat. Hist. **6**, 175–187.

Roberts, A. (1951): The mammals of South Africa. South Africa: The Mammals of South Africa Book Fund.

Rowe-Rowe, D. T.; Meester, J. (1985): Altitudinal variation in external measurements of two small mammal species in the Natal Drakensberg. Ann. Transvaal Mus. **34**, 49–53.

Smithers, R. H. N. (1983): The mammals of the Southern African subregion. Pretoria: Univ. Pretoria.

Yom-Tov, Y.; Nix, H. (1986): Climatological correlates for body size of five species of Australian mammals. Biol. J. Linnean Soc. **29**, 245–262.

Author's address: Prof. Yoram Yom-Tov, Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel